

Effects of functional diversity and functional dominance on complementary light use depend on evenness

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Abstract

Questions: Does functional diversity play a more important role than species richness in complementary resource use? Is the effect of functional diversity on complementarity greater when species evenness is higher? Does functional dominance play an important role in resource use when species evenness is low?

Location: An arable field in Linhai City, Zhejiang Province, China.

Methods: We assembled experimental plant communities with different species richness d-17.7 (.)TJ0.011 Tc o (e)-14.3 (s)-8.2 (s07>,3 (3)4.4 w)TJ/o (eh)-16.fjo)-5.4 (r)-627 (c)0.

was used for the control, and the other for the invasion treatment in which the invaders were added after light measurement of this study. Within each block, 176 plots were established and separated by 1-m wide walkways. The experiment had five levels of species richness (one, two, four, eight and 12 species) and two levels of species evenness (low and high). We used a total of 16 common native species, all occurring in the mountains near Linhai City, to construct the experimental communities in the plots (Supporting Information Appendix S2). All species are biennial or perennial except for *Impatiens* and *Viola*,

which are annuals. In each block, each of the 16 species was planted in monoculture in one plot (total 16 plots), and each of 20 mixtures containing different species combinations were established in two plots for each of the other four species richness levels (i.e. two, four, eight and 12 species, total 160 plots). The species assigned to each mixture were chosen by a random draw from the 16 species. For each species mixture in each block, we created a high evenness community (plot) by assigning equal relative abundance to all species, and created a low evenness community by randomly assigned relative abundance levels to component species (3:1 for two-species mixtures, 8:2:1:1 for four-species mixtures, 12:2:2:2:2:2:1:1 for eight-species mixtures, and 12:2:1:1:1:1:1:1:1:1:1:1 for 12-species mixtures). We used such a low evenness level as grassland communities in the mountains around Linhai City are usually dominated by a single species with a relative density of 47.2% to 78.4%. In the low evenness treatments, the corresponding evenness levels (calculated as E_a ; Alatalo, 1981) were 0.795, 0.632, 0.589 and 0.478 for the two-, four-, eight- and 12-species mixtures, respectively; in the high evenness treatments, all evenness values were 1.

Seeds of the 16 species were collected in the mountains around Linhai City and sown in plastic containers (64 cm × 42 cm × 27 cm) in November 2010 to over winter. In May 2011, seedlings were transplanted into the plots. Each plot was planted with 48 seedlings, and the density was similar to the natural density (40–60 plants/m²) of plant communities in the mountains around Linhai City. In each plot, seedlings of the same species were not placed next to each other, and the 48 seedlings were evenly distributed. Ten days after transplantation, we checked the status of each seedling and the dead ones were replaced. The plots were weeded monthly.

2.3 | Measurements and calculations

In October 2012, we measured four species traits relevant to light capture (plant height, area of a single leaf, leaf angle and cover of a single plant). For measurement, we randomly selected 20 plants and 50 leaves from the monoculture of each species. Leaf area was determined using WinFOLIA (Regent, CA) and leaf angle was measured as the angle between the plane of the leaf and the ground surface. Cover of a single plant was measured by laying 100 cell grids (2.5 cm × 2.5 cm cells in a 10 × 10 grid) over each plant and counting the number of grid cells occupied by the plant. All plants of the two

annuals (*Impatiens* and *Viola*) died during the experiment so that their traits were not measured.

The PAR was measured using a PAR ceptometer (GLZ-C, Zhejiang Top Instrument, China). Three points were randomly selected in the central 0.5 m × 0.5 m area of each plot. Between 11:00–14:00 hr on cloudless days on 1–4 October 2012, PAR above canopy and at ground level were measured at each of the three points. Light interception efficiency (LIE) of a community in a plot was estimated as:

$$LIE = \frac{\text{PAR above community canopy} - \text{PAR at ground level}}{\text{PAR above community canopy}}$$

The mean value of LIE at the three points of a community was used as LIE of the community. Leaf area index (LAI) of the community was determined using an electronic fisheye sensor (LAI 2000; Li-COR, Lincoln, NB, US).

On 21–24 October 2012, we measured species richness in each mixture (communities with more than one species). Due to competition or stochastic deaths of individual plants, species richness observed (S_{observed}) was different from species richness planted, and the maximum value of S_{observed} was 11. Evenness observed was estimated using the relative abundance of each species in the plot. The evenness index of Alatalo (1981) was calculated as follows:

$$E_a = \left(\left(\sum_{i=1}^S P_i^2 \right)^{-1} - 1 \right) / \left(\exp \left(- \sum_{i=1}^S P_i \ln P_i \right) - 1 \right),$$

where P_i is the relative abundance of species i and S_{observed} is the number of species observed in the plot.

We calculated the Euclidean distance between species using the data of the four functional traits of the 14 species (all plants of *Impatiens* and *Viola* died so that no data were available for these two species; Walker, Kinzig, & Langridge, 1999). As the four traits differed greatly in units and scales (Supporting Information Appendix S1), we used the methods of Heemsbergen et al. (2004) for calculation. We first transformed the data of each of the 14 species into rank values (with the smallest value as 1, the second smallest as 2, the third smallest as 3, ..., and the largest as 14) and then calculated the Euclidean distance using the ranks of the four functional traits of the 14 species:

$$d_{ij} = \left[\sum_{k=1}^K (A_{ki} - A_{kj})^2 \right]^{1/2},$$

where d_{ij} is the Euclidean distance between species i and j , and A_{ki} and A_{kj} are the rank values of species i and j for trait k , and K is the number of traits measured (here $K = 4$). Based on the Euclidean distance, we calculated the functional diversity Q index (FD_Q ; Rao, 1982):

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S-1} d_{ij} p_i p_j,$$

where FD_Q is the functional diversity index in a community and p_i and p_j are the relative abundance of species i and j in the community, respectively.

The community-weighted mean (CWM) value of a given functional trait was calculated as (Garnier et al., 2004):

The data of μ , σ and above-ground biomass were analysed with GLM $\mu = 1$

where r_i is the relative abundance of species i in a community, t_i is $t_i^{observed}$ in the community, and t_i is the trait value for species i . t_i was calculated with the trait value of species i divided by the largest trait value among the 14 species (Supporting Information Appendix S1). The trait value ranges from 0 to 1.

We calculated the light complementarity index (C) according to Yachi and Loreau (2007):

where ϵ_i is light interception efficiency of monoculture of species i , ϵ_{mix} is light interception efficiency of mixtures, and $\epsilon_i^{observed}$ of the community. ϵ_i and ϵ_{mix} were, respectively, calculated as:

where ΔE is the light actually intercepted in the community and ΔE_{max} is the maximum light interception of the community. $\Delta E_{mix-max}$ and g were calculated as:

where P_0 is PAR above the community canopy, P_g is PAR at ground level, ϵ_i is the species-specific light interception rate per leaf (ϵ_i is calculated using ϵ_i divided by the total number of leaves of each monoculture of species i), n_i is the largest integer of $\frac{L_i}{L_{mono}}$, L_{mono} is leaf area index of species i in the monoculture, L_{mix} is leaf area index in the mixture and \bar{q} is the average value of q_i for all the species in the mixture.

2.4 | Statistical analysis

Three plots in the high evenness treatment and six plots in the low evenness treatment had no living plants. Monocultures were not included in the regression or correlation analyses as their functional diversity indices were undefined, resulting in a final sample size of 157 high evenness plots (communities) and 154 low evenness plots (communities). Above-ground biomass was harvested after 1 year of light measurement. Because invaders were added to the invasion block after the light measurement, the above-ground biomass in the invasion block was not included in data analysis.

to observed in the high evenness communities ($\rho = 0.210$, $n = 157$, $p < 0.0001$), suggesting that ρ_Q and observed are not independent from each other in the high evenness communities. However, ρ_Q was not positively related to observed in the low evenness communities ($\rho = 0.036$, $n = 154$, $p = 0.681$). $\text{CWM}_{\text{plant height}}$ had no significant relationship with observed in the high ($\rho = 0.105$, $n = 157$, $p = 0.189$) or the low ($\rho = 0.104$, $n = 154$, $p = 0.233$) evenness communities.

The observed did not have any effect on ρ_Q and above-ground biomass (Tables 1 and 2). However, there were significant interactive effects of observed and evenness on ρ_Q and $\text{CWM}_{\text{plant height}}$ (Table 1; for ρ_Q , $\chi^2 = 4.591$, $p = 0.032$; for $\text{CWM}_{\text{plant height}}$, $\chi^2 = 6.934$, $p < 0.001$), and there was a marginally interactive effect of observed and evenness on above-ground biomass (Table 2: for above-ground biomass, $\chi^2 = 3.843$, $p = 0.071$). observed was positively related to ρ_Q and above-ground biomass (Figures 1a and 3a) in the high evenness communities, but not in the low evenness communities (Figures 1d and 3d).

The ρ_Q significantly affected $\text{CWM}_{\text{plant height}}$ and $\text{CWM}_{\text{plant height}}$ (Table 1). As indicated by a significant interaction between evenness and ρ_Q (Table 1: for ρ_Q , $\chi^2 = 14.780$, $p < 0.001$; for $\text{CWM}_{\text{plant height}}$, $\chi^2 = 10.107$, $p < 0.001$; Table 2: for

FIGURE 1 Relationships of light interception efficien

Communities with higher species richness have a higher possibility of having species with some specific trait values, such as , and in our study. Consequently, the trait

difference between these species and others will be larger and leads to higher functional diversity. We also found that both species richness and functional diversity promoted light inception efficiency ()

2014). These dominant species contribute to most of the community biomass and thus are likely to play a key role in resource use and ecosystem functioning (Sasaki & Lauenroth, 2011; Smith & Knapp, 2003). In this study, taller plant species (*Pinus*, *Quercus* and *Populus*) had a higher ability for light competition and thus intercepted most of the light. Consequently, the presence of these dominant species led to positive relationships between $CWM_{\text{plant height}}$ and light use in the low evenness communities. As functional diversity and functional dominance are not exclusive and simultaneously influence ecosystem functioning (Mensah et al., 2016), we postulate that increasing species evenness increases the role of functional diversity but decreases that of functional dominance.

4.3 | Roles of species with the greatest initial abundance in resource use

We found that light use of the low evenness communities was positively correlated with light use of the monocultures consisting of the species with the largest initial abundances and light use of the low evenness communities was negatively correlated with it. Differences in functional traits among species reflect differences in competitive abilities of the species to capture resources, and thus such inter-specific trait differences stand for trait competitive hierarchy among species (Kunstler et al., 2012, 2016; Mayfield & Levine, 2010). Consequently, trait competitive hierarchy of the most abundant species may greatly affect resource complementary use (Legner, Fleck, & Leuschner, 2013; Lorentzen, Roscher, Schumacher, Schulze, & Schmid, 2008). In this study, the low evenness communities were artificially constructed with species of different initial abundances. When taller and larger plant species have larger initial abundances (such as *Pinus*, *Quercus* and *Populus*), they can preempt light over shorter and smaller plants (Falster & Westoby, 2003; Freckleton & Watkinson, 2001; Roscher, Schumacher, Schmid, & Schulze, 2015; Weiner & Damgaard, 2006). As a result, light complementary use is lower in such low evenness communities compared to that in the high

evenness communities due to a limited contribution from the shorter and smaller species for their little initial abundance and competitive disadvantage (Anten & Hirose, 1999). In contrast, when shorter and smaller species have larger initial abundances (such as *Trifolium* and *Lotus*), light complementary use is higher in such low evenness communities than in the high evenness communities due to a disproportionate contribution from the taller and larger species to light use. This explains why light use of the low evenness communities was negatively correlated with light use of the monocultures ($r = -0.625$, $T < 0.05$, $Df = 4$) ($h = -15.7916$) ($l = 5.9$) ($i = 7.1$) ($g = 2.47$) ($op = 6$) (one-tailed test).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Experimental treatments with five levels of species richness (1, 2, 4, 8 and 12 species) and two levels of evenness (high and low)

Appendix S2 The characteristics of 16 species used in the experiment. Family, life form and four functional traits (mean \pm) related to light interception were given

Appendix S3 Correlations among CWM value of the four traits (plant height, area of a single leaf, leaf angle and cover of single plant)

Appendix S4 Relationships of light interception efficiency () with CWM value of area of a single leaf ($CWM_{\text{area of a single leaf}}$), (b, e) leaf angle ($CWM_{\text{leaf angle}}$) and cover of a single plant ($CWM_{\text{cover of a single plant}}$) in the high and low evenness communities

Appendix S5 Relationships of light complementarity index () with CWM value of area of a single leaf ($CWM_{\text{area of a single leaf}}$), leaf angle ($CWM_{\text{leaf angle}}$) and cover of a single plant ($CWM_{\text{cover of a single plant}}$) in the high and low evenness communities

Appendix S6 The relationship between plant height of the species with the largest initial abundance and light interception efficiency of their monocultures

Appendix S7 Coefficient of correlation of light interception efficiency with the functional diversity Q index (Q_{α}) at each level of observed species richness (S_{observed}) and with S_{observed} at each level of Q_{α}

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